

BEHAVIORAL FLEXIBILITY IN ORB WEB CONSTRUCTION: EFFECTS OF SUPPLIES IN DIFFERENT SILK GLANDS AND SPIDER SIZE AND WEIGHT

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ABSTRACT

Comparisons of webs spun in the field when both sticky and non-sticky silk supplies were complete, when both were recently depleted, and when only non-sticky supplies were depleted show that *Leucauge mariana* and *Micrathena sexspinosa* vary design features of their orbs such as numbers of radii and sticky spiral loops, web area and proportion covered with sticky spiral, sticky spiral symmetry, and spaces between sticky spiral loops in response to changes in the amounts of both sticky and non-sticky silk that they have available. Spider size, spider weight and possibly website also influence *L. mariana* web designs.

INTRODUCTION

The orbs of araneid spiders are composed of a sticky spiral, produced by the aggregate and flagelliform glands, and a network of non-sticky supporting lines (radii, frames, hub and temporary spiral) drawn from the ampullate glands (Kovoor 1977; Kavanagh and Tillinghast 1979). Several aspects of orb web design have been thought to be species- or genus-specific (Savory 1952; Witt and Baum 1960; Reed and Jones 1965; Witt et al. 1968; Risch 1977; Foelix 1982; Ramousse and LeGuelte 1984; Tyshchenko 1984). Individual spiders appear however, to adjust some web characteristics on the basis of their silk supply. Laboratory experiments using drugs that stimulated non-sticky silk production altered orb sizes and designs (Witt et al. 1968), as did manipulation of non-sticky silk production by altering the spider's demands for non-sticky silk (Reed et al. 1970). These studies did not take into account, however, other possible effects of the drugs, or possible effects of changes in silk supplies in other glands. The present report of field observations of the araneids *Leucauge mariana* (Keyserling) and *Micrathena sexspinosa* (Hahn) shows that recent expenditure of sticky as well as non-sticky silk influences web designs. Spider size, spider weight and possibly websites are also shown to influence web design in *L. mariana*.

MATERIALS AND METHODS

Individual spiders were followed during the course of a day by marking websites rather than spiders, as spiders were generally several meters from each

other, and usually did not change sites during the day (spiders that did move were not included). *L. mariana* was observed in second growth near San Antonio de Escazu, San José Province, Costa Rica, and *M. sexspinosa* at the edge of a large clearing at the La Selva field station near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica. All individuals observed were mature females. Webs were measured in the field, and then collapsed by cutting all but three radii near their outer ends with a scissors, leaving all silk still in the web, and the frame and anchor lines intact. Web area was estimated by multiplying vertical length times horizontal width measured from frame to frame. By weighing paper cutouts of 53 photographed *L. mariana* webs, it was determined that such estimates correlate strongly with area ($r = 0.80$). The number of sticky loops was the average of the number above and below the hub in *M. sexspinosa*, and the average of those above, below, and to the right and left of the hub in the less symmetrical webs of *L. mariana*. The average space between sticky spiral loops was the distance from the inner to the outer loop divided by the number of loops.

Those *L. mariana* spiders which were to be weighed were placed in individual plastic vials with fresh leaves within 1-2 hours of finishing their first webs of the day, and weighed to the nearest 0.1 mg less than 12 hours later on an electrical balance. Using the average rate of weight loss for nine spiders kept in vials for seven hours (0.05 mg/h—spider weights averaged about 45 mg), each spider's estimated weight when it spun its web was calculated. Each spider was placed in alcohol after being weighed, and cephalothorax and tibia I lengths were measured later using a dissecting microscope.

Website effects on orb design were investigated by measuring the first webs of the day for a series of spiders. These spiders were then removed (with little or no damage to the webs) and were replaced the same morning by other spiders taken from finished orbs of their own; the first webs made by the replacement spiders at the same sites were measured the next morning.

When possible, statistical tests were performed comparing different webs spun by the same spider on the same day and at the same site, allowing the spider to act as its own control.

RESULTS

Normal webs.—Both *L. mariana* and *M. sexspinosa* replaced damaged webs 1.5-10 hours after their original webs were destroyed at 0700-0900 hours. The second, replacement webs of both species were consistently smaller in area, had fewer radii, and fewer loops of sticky spiral (Table 1). The average spaces between sticky spiral loops were unchanged. Third webs of *L. mariana* spun the same day to replace destroyed second webs (all third webs were built <15 hours after the first web) showed further reductions in numbers of radii and loops, increased spaces between loops, but no further change in web area (Table 1).

The relative portion of *L. mariana* webs within the outermost loop of sticky spiral also varied. The distances from the outermost sticky loops to the outer ends of the radii were greatest in third, smaller in second, and smallest in first webs (Fig. 1) (first and second webs differed comparing numbers of distances both <0.6 cm and >1.5 cm with Chi Square— $p < 0.05$, $p < 0.001$ respectively); second and third differed comparing both <1.1 and >2.0 cm—both $p < 0.001$ with Chi Square).

Table 1.—Averages and standard deviations of characteristics of normal first, second and third webs and experimental second webs, and statistical comparisons of ratios from webs spun by the same spiders on the same days at the same sites (two sets of first webs are used in the comparisons of *L. mariana* webs). Differences between values followed by the same letter are highly significant ($p < 0.001$) with Mann-Whitney *U*-test.

Web	Number of Radii	Number of Sticky Loops	Area (cm) ²	Space Between Loops (cm)	<i>N</i>
<i>Micrathena sexspinoso</i>					
First	38.3 ± 7.1	25.0 ± 6.5	367 ± 190	0.23 ± 0.04	121
Second	26.2 ± 4.4	19.3 ± 4.6	286 ± 101	0.24 ± 0.04	50
Experimental	32.0 ± 4.6	24.3 ± 4.5	416 ± 148	0.25 ± 0.06	37
Second/First	0.66 ± 0.16a	0.75 ± 24	0.80 ± 31b	1.06 ± 0.15	45
Exptl. / First	0.83 ± 0.09a		1.09 ± 0.31b		35
<i>Leucauge mariana</i>					
First	30.2 ± 3.3	41.2 ± 10.2	670 ± 222	0.23 ± 0.03	80
Second	23.4 ± 2.7	27.4 ± 4.9	453 ± 250	0.24 ± 0.04	78
Third	20.7 ± 3.0	22.3 ± 4.5	403 ± 150	0.26 ± 0.07	40
Experimental	26.2 ± 3.4	35.5 ± 7.2	549 ± 255	0.22 ± 0.04	29
Second / First	0.79 ± 0.11c	0.70 ± 0.14d	0.64 ± 0.18	1.01 ± 0.13e	40
Third / First	0.62 ± 0.12c	0.53 ± 0.14d	0.65 ± 0.20	1.24 ± 0.25e	40
Second / First	0.82 ± 0.08f	0.67 ± 0.09	0.68 ± 0.19g	1.05 ± 0.14	29
Exptl. / First	0.92 ± 0.07f		0.96 ± 0.28g		29

Sticky spiral asymmetry was reduced in second and third *L. mariana* orbs. Absolute values of differences between the average number of loops and the numbers of loops in the four sectors were summed for each web in 44 cases in which the same spider made three successive webs at the same site on the same day. The sums for first webs ($\bar{x} = 8.4 \pm 5.0$) were larger than those in second ($\bar{x} = 5.0 \pm 4.6$) and third ($\bar{x} = 4.4 \pm 4.2$) webs (both $p < 0.001$ with Mann-Whitney *U*-test). In addition, when the difference between the maximum and minimum number of loops in each web were compared between first, second and third webs, those in first webs ($\bar{x} = 5.8 \pm 3.3$) were larger than those in second ($\bar{x} = 3.4 \pm 3.2$) and third ($\bar{x} = 3.0 \pm 2.7$) webs (both $p < 0.001$ with Mann-Whitney *U*-test), and the proportion of webs with differences of >4 loops was greater among first than in second or third webs (both $p < 0.001$ with Chi Square). Since spiders often reused frame lines from previous webs, the sticky spirals of later orbs may have been more symmetrical because these webs tended to have relatively larger frame areas as compared to sticky spiral areas, making fewer turnbacks in the sticky spiral necessary (Eberhard 1969).

Experimental modification of relative amounts in glands.—The relative amounts of sticky and non-sticky silk available to the spider when the second web was begun were modified experimentally by allowing the spider to finish adding non-sticky lines to the first web (radii, frame, hub, temporary spiral), but then cutting the radii as above, thus preventing the spider from laying any sticky silk. The spider's non-sticky silk supply was thereby reduced, while the sticky silk supply was left intact. The experimental second webs that followed did not have reduced areas; they had fewer radii and, in *L. mariana*, fewer sticky loops than first webs, but the reductions in both were significantly less than those in normal second webs of both species (Table 1). The relative portion of the web enclosed within the outermost sticky spiral loop was not reduced as in normal second webs

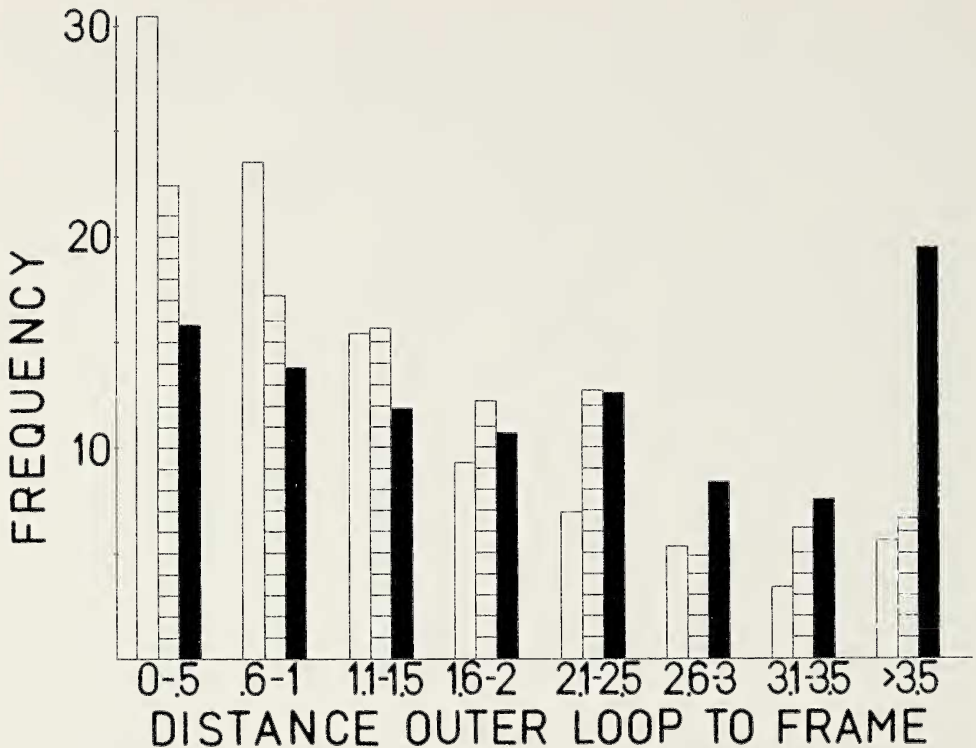


Fig. 1.—Frequencies of distances between outer loops of sticky spiral and ends of radii in normal first (white), second (hatched) and third (black) webs ($N = 44$ in each case) that were spun by *L. mariana* females (three webs/female, all on the same day). Distributions are significantly different with Chi-Square Test.

(predicted distances from outer loops were calculated for experimental webs using the percentages for normal second webs in Fig. 1).

By cutting radii as soon as they were laid, *L. mariana* spiders were experimentally induced to lay more than one additional set of radii during construction of replacement webs (radii represent approximately 20-30% of the non-sticky silk in a finished orb—Eberhard 1986), confirming that orb construction of normal second webs does not completely empty the ampullate glands of this species, just as in the first webs of *Araneus diadematus* Clerck (König 1951; Witt et al. 1968), *L. mariana* and *Gasteracantha cancriformis* (Linnaeus) (Eberhard 1986), and the unidentified araneid studied by Hingston (1920).

Correlations with spider size and weight.—Correlations between spider size and weight and dimensions of first webs of 138 *L. mariana* showed that larger and heavier spiders made webs with more closely spaced sticky spiral loops, and somewhat larger webs (Table 2). Partial correlations showed that both weight and a combination of body size measures ($x = \text{tibia} / \text{average tibia} + \text{cephalothorax} / \text{average cephalothorax}$) had significant correlations with sticky spiral spacing (partial correlation coefficients were -0.26 and -0.23 respectively, both $p < 0.001$). Partial correlations with web area were not significant.

Website effects.—There were strong positive correlations between the slants and areas of successive webs at the same site spun by different spiders ($r = 0.46$, $p <$

Table 2.—Correlation coefficients between web and body measurements of 138 adult female *Leucauge mariana* (* $p < 0.05$, ** $p < 0.001$).

	Area	Number Sticky Loops	Space between Sticky Loops	Number Radii	Slant
Cephalothorax	0.206*	-0.065	-0.358**	-0.056	-0.124
Tibia	0.172	-0.100	-0.343**	-0.027	-0.055
Wet weight	0.267**	0.033	-0.399**	0.006	-0.117

0.001 and $r = 0.335$, $p < 0.01$ respectively for 63 pairs of webs). Other web features showed no significant relationships, nor was there a significant correlation between the weights of successive spiders occupying the same sites.

DISCUSSION

It might be thought that differences between first and second webs were due to the first webs usually being spun in darkness and the second in daylight (Ramousse and LeGuelte 1979 on *Araneus diadematus*). The differences between second and third webs of *L. mariana* and experimental and second webs of both species (all built during the day) indicate however that light conditions during construction do not explain the changes in design.

The reduced numbers of radii in both normal and experimental second orbs of *L. mariana* and *M. sexspinosa* suggest that, as in *A. diadematus*, non-sticky silk in the ampullate glands probably influences their web designs. The experimental webs show, however, that the supply of sticky silk can partially "over-rule" the effect of non-sticky silk availability. *A. diadematus* may also respond to cues from its sticky silk glands. Preliminary evidence shows similar reductions may occur in radius and sticky spiral loop number and web area when webs are built in close temporal succession (Ramousse 1977). Slight reductions of numbers of sticky spiral loops occurred in webs spun by spiders which had been milked of non-sticky silk, but prevented from laying sticky silk for three weeks (presumably gland output was reduced when demand ceased) as compared with controls which had spun normal webs (21.0 vs. 26.5, $N = 6$ for both, significance levels were not given) (Reed et al. 1970).

Sticky silk forms a large fraction of an orb. Its length ranged from about 36 to 54% of the total length of silk in more or less typical orb designs (Eberhard 1986). By weight it may be an even larger fraction. The non-sticky scaffolds of *Argiope aurantia* webs weighed only about 16% of the dry weight of the finished orb (Tillinghast et al. 1984). Taking into account the non-sticky stabilimentum, which was included along with the sticky spiral in the remaining 84%, it is probable that the sticky lines account for 70-80% of the dry weight of an orb (E. K. Tillinghast, pers. comm.). Sticky silk is also, of course, a key web component in trapping prey. In sum, it is perhaps not surprising that the supply of sticky silk influences web design. The relatively smaller portions of later webs occupied by sticky spiral, the big proportion occupied in experimental second webs, and the spiders' ability to lay many extra radii during second web construction all suggest that sticky rather than non-sticky silk sometimes limits web size (see also Eberhard 1986).

It is tempting to postulate that non-sticky gland contents determine the design of non-sticky web components, and sticky silk supplies affect sticky silk design features. There are, however, probably "crossovers" in cues from the two types of glands; for instance, web area (a design feature of non-sticky lines) was not reduced in experimental second webs of either species, even though supplies of non-sticky silk had been reduced.

Individual araneids sometimes produce non-sticky lines with varying diameters (e.g., Christiansen et al. 1962; R. W. Work pers. comm.), and the sizes and spaces between sticky balls on the sticky spiral of *L. mariana* webs varies substantially even within a single web (Eberhard unpub.). Thus the web measurements given here may not accurately reflect total amounts of material in different webs. The probable trend in diameter modification (smaller diameters when gland less full) suggests that the trends documented here give underestimates of the differences in the amount of material in successive webs.

Several previous studies have analyzed the relationships between spider size and weight, but many comparisons include the possibly confounding effects of species or age (instar) differences. Comparisons of webs of conspecific mature females with different weights (Christiansen et al. 1962; Risch 1977) and different body sizes (Risch 1977) suggest that both factors have effects on web design in other araneid species. Variations in *L. mariana* web designs associated with greater spider weight were similar to those associated with relatively greater supplies of sticky silk (decreased spaces between sticky loops, greater area), but differed in showing no relations with numbers of radii or sticky loops (Table 1). Larger spider weights might be associated to some extent with greater recent feeding success and thus, presumably, greater amounts of material in the glands, but a female spider's weight is probably largely determined by the stage of development of its eggs. Thus the weight effects documented here may be largely independent of the gland-filling effects.

Website may be still another factor causing *L. mariana* web designs to vary. Spiders often reuse some of the frame lines from previous webs (Eberhard, unpub.), and the correlations in slant and area of successive first webs could be due to frame reuse. It is also possible that other website characteristics were important. Adjustments of web design to local conditions are undoubtedly advantageous for orb weavers; they are suggested by field data (Leborgne and Pasquet 1987), and have been documented in confinement (Tilquin 1942; Szlep 1958; LeGuelte 1966).

The intraspecific variations documented here are substantial. For instance, even when one controls for possible effects of spider size, weight, and website in *L. mariana*, first webs average 146% more radii, 185% more sticky spiral loops, and 166% more area than third webs; some individual spiders, of course, showed even greater variations. The magnitude of this variation, the existence of similar variation in other species (Ramousse and LeGuelte 1979; Leborgne and Pasquet 1987), and the correlations between these and other web characters (Leborgne and Pasquet 1987) weaken the old hope that orb designs can provide reliable species-specific characters (e.g., Savory 1952; Foelix 1982). If such web characters exist, they may be associated with more subtle details such as number and pattern of hub loops, relative size of free zone, etc. (see Coddington 1986 for examples of useful generic characters in webs of Theridiosomatidae). It is possible that different species have different ways of adjusting to changes in factors such as

supplies of sticky and non-sticky silk and spider size and weight, but proof of this will require much more information that is presently available. Intraspecific variation seen in other studies. (LeGuelte 1966; Risch 1977; Ramousse and LeGuelte 1979, 1984; Nentwig 1983, 1985; Tyschenko and Marusik 1985, Tyshchenko et al. 1985; Buskirk 1986; Leborgne and Pasquet 1987) may be due at least in part to the factors discussed here.

In light of these findings, the probable nervous mechanisms controlling orb construction appear to be extraordinarily complex. Both internal factors (weight, body size, contents of sticky and non-sticky silk glands) and external factors (website and/or previous lines present there) are integrated in determining a variety of design features, ranging from basic characteristics such as numbers of radii and sticky loops and web area, to more subtle aspects such as the relative symmetry of the sticky spiral and the relative fill of the web area with sticky spiral. Different features are modified at least partially independently. The influence of gland contents and perhaps that of the website may incorporate feedback loops involving amounts of silk and web designs used previously (Reed et al. 1970; Tillinghast and Townley 1986; this study). During actual construction several other factors, such as gravity, leg length and distances and angles between lines, and memories of distances and directions travelled (Hingston 1920; Tilquin 1942; LeGuelte 1966; Vollrath 1986, 1987; Eberhard 1987, 1988) also influence the paths taken and the lines laid. The reasons why spiders opt for different orb designs when they have different amounts of silk available are not yet clear; but there is no doubt that we must discard once and for all the old image of orb weaving spiders spinning out the same rigidly programmed, inflexible geometric patterns in their webs day after day.

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LITERATURE CITED

- Buskirk, R. 1986. Orb-weaving spiders in aggregations modify individual web structure. *J. Arachnol.*, 14:259-265.
- Coddington, J. A. 1986. The genera of the spider family Theridiosomatidae. *Smithsonian Contrib. Zool.*, 422:1-96.
- Christiansen, A., R. Baum and P. N. Witt. 1962. Changes in spider webs brought about by mescaline, psilocybin, and an increase in body weight. *J. Pharmac. exp. Ther.*, 136:31-37.
- Eberhard, W. G. 1961. Computer simulation of orb-web construction. *American Zool.*, 9:229-238.
- Eberhard, W. G. 1986. Effects of orb-web geometry on prey interception and retention. Pp. 70-100, *In Spiders—Webs, Behavior and Evolution* (W. A. Shear, ed.). Stanford Univ. Press, Stanford.
- Eberhard, W. G. 1987. The effect of gravity on temporary spiral construction by the spider *Leucauge mariana* (Araneae, Araneidae). *J. Ethol.*, 5:29-36.
- Eberhard, W. G. 1988. Memory of distances and directions moved as cues during temporary spiral construction in the spider *Leucauge mariana* (Araneae: Araneidae). *J. Insect Behav.*, 1:51-66.
- Foelix, R. 1982. *Biology of Spiders*. Harvard Univ. Press, Cambridge.

- Hingston, R. W. G. 1920. *A Naturalist in Himalaya*. H. F. & G. Willoby, London.
- Kavanagh, E. and E. K. Tillinghast. 1979. Fibrous and adhesive components of the orb webs of *Araneus trifolium* and *Argiope trifasciata*. *J. Morph.*, 160:17-25.
- König, M. 1951. Beiträge zur Kenntnis des Netzbaues orbteiler spinnen. *Z. Tierpsychol.*, 8:462-492.
- Kovoor, J. 1977. La soie et les glandes sericigenes des arachnides. *Ann. Biol.*, 16:97-171.
- Leborgne, R. and A. Pasquet. 1987. Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). *Behav. Ecol. Sociobiol.*, 20:203-208.
- LeGuelte, L. 1966. Structure de toile de *Zygiella x-notata* Cl. (Argiopidae) et facteurs que regissent le comportement de l'araignee pendant la construction de la toile. These Publ. Univ. Nancy, Nancy.
- Nentwig, W. 1983. The non-filter function of orb webs in spiders. *Oecologia (Berlin)*, 58:418-420.
- Nentwig, W. 1985. Prey analysis of four species of tropical orbweaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia (Berlin)*, 66:580-595.
- Ramousse, R. 1977. Organisation spatio-temporelle du comportement constructeur chez *Araneus diadematus* (Araignee, Argiopidae). Thèse Univ. Claude-Bernard de Lyon, Lyon.
- Ramousse, R. and L. LeGuelte. 1979. Relations spatio-temporelles dans le comportement constructeur chez l'*Epeira diademe*. *Rev. Arachnol.*, 2:183-192.
- Ramousse, R. and L. LeGuelte. 1984. Strategies de construction de la toile chez deux especes d'araignees (*Araneus diadematus* et *Zygiella x-notata*). *Rev. Arachnol.*, 5:255-265.
- Reed, C. F. and R. L. Jones. 1965. The measuring function of the first legs of *Araneus diadematus* Cl. *Behaviour*, 25:98-119.
- Reed, C. F., P. N. Witt, M. Scarboro and D. B. Peakall. 1970. Experience and the orb web. *Develop. Psychobiol.*, 3:251-265.
- Risch, P. 1977. Quantitative analysis of orb-web patterns in four species of spiders. *Behav. Genet.*, 7:199-238.
- Savory, T. H. 1952. *The Spider's Web*. Frederick Warne, London.
- Szlep, R. 1958. Influence of external factors on some structural properties of the garden spider (*Aranea diademata*) web. *Folia Biol. (Praha)*, 6:287-299.
- Tillinghast, E. K., S. F. Chase and M. A. Townley. 1984. Water extraction by the major ampullate duct during silk formation in the spider *Argiope aurantia* Lucas. *J. Insect Physiol.*, 30:591-596.
- Tillinghast, E. K. and M. A. Townley. 1986. The independent regulation of protein synthesis in the major ampullate glands of *Araneus cavaticus* (Keyserling). *J. Insect Physiol.*, 32:117-123.
- Tilquin, A. 1942. *La Toile Geometrique des Araignees*. Presses Univ., Paris.
- Tyshchenko, V. P. 1984. The catching webs of orb-weaving spiders 1. The substantiation of the method of standard webs with reference to two species of the genus *Araneus* (Aranei, Araneidae). (in Russian) *Zool. Zhurnal*, 63:839-847.
- Tyshchenko, V. P. and Y. M. Marusik. 1985. Catching webs of orbweaving spiders 3. Geographic variation of webs in *Araneus marmoreus* (Aranei, Araneidae). (in Russian) *Zool. Zhurnal*, 64:1816-1822.
- Tyshchenko, V. P., Y. M. Marusik and C. K. Tarabaev. 1985. The catching webs of orb-weaving spiders 2. Comparative study of the webs in the genus *Nuctenea* (Aranei, Araneidae). (in Russian) *Zool. Zhurnal*, 64:827-834.
- Vollrath, F. 1986. Gravity as an orientation guide during web-construction in the orb spider *Araneus diadematus*. *J. Comp. Physiol.*, 159:275-280.
- Vollrath, F. 1987. Altered geometry of webs in spiders with regenerated legs. *Nature*, 328:247-248.
- Witt, P. N. and R. Baum. 1960. Changes in orb webs of spiders during growth (*Araneus diadematus* Clerck and *Neoscona vertebrata* McCook). *Behaviour*, 16:309-318.
- Witt, P. N., C. F. Reed and D. B. Peakall. 1968. *A spider's web*. Springer Verlag, New York.

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